BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. AUGUST 11, 1972 NUMBER 389

THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIII. AN EARLY ORNITHOSUCHID PSEUDOSUCHIAN, *GRACILISUCHUS STIPANICICORUM*, GEN. ET SP. NOV.

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ABSTRACT. A description is given of the skull and skeleton of a small ornithosuchid thecodont, *Gracilisuchus stipanicicorum* gen. et sp. nov., from the Triassic (? Anisian) Chañares Formation of Argentina. The skull is of an advanced pseudosuchian character, with a large antorbital opening, a very large orbit and a lateral temporal opening of an advanced type. The front limbs are short, being about 3/5ths the length of the hind; the tibia is nearly as long as the femur. Armor consisted of a double row of dorsal scutes.

INTRODUCTION

Work in the Triassic of Argentina and southern Brazil in recent decades has resulted in the discovery of a considerable number of new thecodonts; some 21 genera have now been described from the Triassic of this area. Most are known from incomplete remains; however, in the last paper in this series (Romer, 1972), I have been able to give a fairly complete skeletal restoration of the long-snouted *Chanaresuchus*, and below I give a description of the nearly complete skull and skeleton of a small ornithosuchid.

Gracilisuchus stipanicicorum, gen. et sp. nov.

Combined generic and specific description. A small ornithosuchid, with a skull length on the order of 95 mm and a presacral column of 23 segments, with a length of about 21 cm. Skull of advanced pseudosuchian type. Premaxillae extending upward back of nares, excluding the maxillae from that opening. Antorbital fenestra large, included in a recessed area of

maxilla and lacrimal; antorbital bar moderately narrow. No pineal opening; a tiny postparietal bone present. V-shape of lateral temporal opening so pronounced that the upper part of the opening is closed by apposition of squamosal to postorbital and jugal. Basicranial kineticism lost; the pterygoids meet medially beneath the basisphenoid region. Lateral flanges of pterygoids highly developed, extending directly outward the entire width between lower jaws. Normal stance possibly bipedal; femur and tibia combined about 1 1/2 times skull length and about 1 2/3 the length of humerus plus radius; tibia and fibula somewhat shorter than femur. Dorsal scutes are about 1/2 vertebral length and paired, each element having a vertical lateral portion and a horizontal median flange that overlaps its mate.

The generic name refers to the obviously graceful build of the little reptile. The specific name is in honor of Drs. Pedro and Maria Stipanicic, able students of Triassic stratigraphy and palaeobotany.

I am indebted to National Science Foundation grant GB-2454 for aid in the collecting of the specimen and grant GB-22658 for preparation and publication.

Holotype. La Plata Museum No. 64-XI-14-11 (Field no. 146). A slab (Fig. 1) exhibiting a skull in dorsal view, much of the presacral column and scattered limb and girdle material. Also present on the slab is the type material of *Lagosuchus talampayensis* (Romer, 1971), and originally a gomphodont skull was likewise present. Collected from the Chañares Formation in La Rioja Province, Argentina, about 2 km north of the Rio Chañares.

Other material. A number of further Chañares specimens include remains of the present animal. These are:

MCZ[1] 4117 (Field no. 153, *partim*). A nearly complete skull and jaws from the same locality as the holotype.

MCZ 4118 (Field no. 153, *partim*). In the same nodule as the last, but separated from it by a short distance, was a specimen including ventral elements of the skull, the jaws and a partial postcranial skeleton, including a well-preserved cervical region.

MCZ 4116 (Field no. 174). A slab including a crushed skull and jaws and considerable postcranial material, part of it pertaining to a smaller reptile. From the holotype locality.

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Further *Gracilisuchus* material, collected by Sr. José Bonaparte, is in the Instituto Lillo, Tucumán. Notable is a specimen with an incomplete skull and the greater part of a skeleton that agrees with *Gracilisuchus* in all identifiable features; the individual is about 20 percent larger than the holotype.

CRANIUM

(Figures 1-4)

Cranial materials are present in all four specimens listed above. The skull in MCZ 4117 is nearly completely preserved, except for the palate, and is uncrushed. In the holotype the skull roof and right side of the face are seen on the upper side of the slab; ventrally there is present part of the palate and the disarticulated left maxilla and jugal. In MCZ 4118 the ventral margins of the skull and complete lower jaws are preserved. In MCZ 4116 the right aspect of the skull, crushed and elements disarticulated, is seen on one surface; on the opposite surface are disarticulated elements of the left side.

Skull length to the posterior end of the table is 85 mm in MCZ 4117, and appears to have been similar in the holotype and in 4116 and 4118. The general proportions are those to be expected in a moderately advanced pseudosuchian. As viewed dorsally, the shape is essentially triangular, expanding gradually from a slender snout to a greatest width across the temporal region. Anteriorly the skull outline curves up sharply above the external nares, but from this point backward there is little further increase in height, the roof being essentially flat and the height nowhere great. The external nares are moderately large. The facial length is not excessive, the distance from snout to orbital margin being somewhat less than half the total skull length. The antorbital vacuities are large, and set in an oval recess, which is bounded anteriorly by a pronounced curved line running upward along the maxilla; it is deeply overhung dorsally by the prominent lateral edge of the skull roof. The orbit is very large, its diameter being about 1/3 the skull length. It not only occupies nearly the entire height of the face, but also extends medially across much of the dorsal surface of the skull. The temporal region, in contrast, is short. The superior temporal fenestra is triangular in shape, narrow anteroposteriorly but extending broadly outward behind the postorbital bar. The lateral temporal opening is of unusual structure. As in advanced thecodonts generally, the posterior border is V-shaped, the apex of

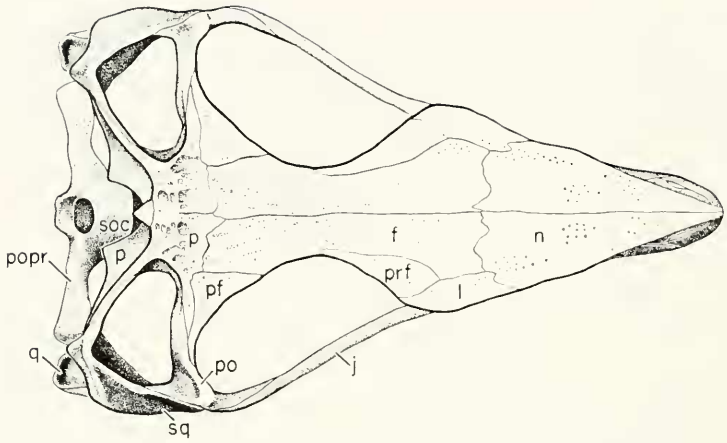

Figure 1. The skull in dorsal view. This and the following skull figures are based mainly on MCZ 4117 × 1. Abbreviations for Figs. 1 to 5: *a*, articular; *an*, angular; *c*, coronoid; *d*, dentary; *ec*, ectopterygoid; *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *part*, prearticular; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *popr*, paroccipital process; *pp*, postparietal; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *san*, surangular; *soc*, supraoccipital; *sp*, splenial; *sq*, squamosal.

the V pointing anteriorly. Here, however, in contrast to normal advanced forms, the forward push of the V is so pronounced that the upper limb of the V is in contact with the postorbital and jugal; as a consequence the upper half of the fenestra is completely closed, the opening remaining being a ventral triangular area. A similar situation is present in the aetosaurs.

The premaxillae are thickened ventrally, with accommodation for tooth roots. Anteriorly each element sends a slender process upward to meet the nasal medial to the narial openings. Posteriorly the premaxilla sends a stout process upward to form part of the posterior border of the naris.

A pronounced ridge extends backward on either side of the skull roof along the upper margin of the antorbital region toward the upper anterodorsal margin of the orbit; this pair of ridges, formed anteriorly by the nasals, sharply separates the flattened dorsal surface of the skull from the essentially vertical lateral surfaces. Below this ridge the nasal extends downward to form the upper boundary of the naris. This flange is in contact with the premaxilla ventrally, both in front of and behind the naris. On the dorsal surface the nasals extend well backward, broad-

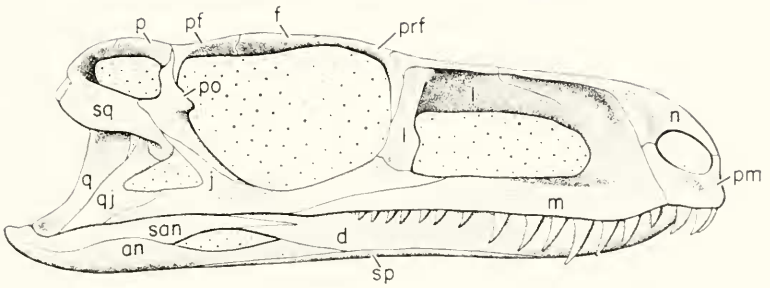

Figure 2. The skull in lateral view. × 1.

ening posteriorly. The lateral ridges form their lateral boundaries for most of this distance; part way along the upper margin of the facial region, however, the width of the nasals is somewhat constricted by the presence of the lacrimals. Nasals and frontals meet in a broad transverse suture, not readily discernible, a short distance anterior to the anterior margin of the orbits.

The frontals are elongate, their length being roughly that of the large orbits. Broad anteriorly, they are constricted in width by the strong medial curvature of the dorsal orbital margins, the prefrontals being interposed for some distance between them and the frontals. Posteriorly the frontals are bounded laterally by the postfrontals, and terminate at an irregular transverse suture with the parietals.

The last elements are short in longitudinal extent, occupying, roughly, only the length of skull roof opposite the short temporal region. There is no pineal opening; posteriorly the median suture is absent. Laterally the parietals send out a flange on either side, anterior to the superior temporal fenestra and behind the postfrontal, to gain a postorbital contact. Posterior to the upper fenestra the parietals send out on either side strong flanges that form the upper margins of the occipital surface and, along the posterior margins of the fenestrae, overlap posteriorly ascending flanges of the squamosals.

The postparietal, seen on MCZ 4117, persists as a small triangular wedge of bone that projects strongly backward from the middle point of the dorsal occipital surface; it is essentially the most anterior portion of the dorsal armor that continues down the back.

The maxilla is prominently developed. Its major ramus is a long strip of bone that carries the tooth bases and extends backward from a premaxillary contact to a point not far forward of

the posterior border of the orbit. Anteriorly it forms the lower margin of the antorbital fenestra. Near the posterior limit of the fenestra the anterior end of the jugal is found above the maxilla, and from this point back the maxilla is reduced, to become a slender splint. Anteriorly the maxilla fails to reach the external naris. It sends upward a broad process, bounded posteriorly by the antorbital vacuity and anteriorly by the premaxilla, from which it is separated by a very prominent incised suture. Curving upward along the surface of this process is a well-marked ridge separating the proper outer surface from the depressed area in which the antorbital vacuity develops. Dorsally this maxillary process extends backward below the lateral skull ridge to form part of the upper margin of the antorbital vacuity.

The lacrimal forms most of the vertical bar of bone between orbit and antorbital vacuity. This bar is of limited width; it has a conspicuous ridge along its anterior border, and a less developed ridge posteriorly. Below, the lacrimal meets the jugal. Above, the lacrimal forms the projecting process between the orbital rim and the lateral ridge above the facial region, and extends forward above the antorbital opening. It has (unusually) a modest exposure on the dorsal surface, lateral to frontal and nasal. The prefrontal is a small wedge-shaped element, lateral to the frontal and posterior to the dorsal exposure of the lacrimal; it forms the anterior half of the curved dorsal margin of the orbit.

The postfrontal is a triangular element of modest size, lying above the posterodorsal margin of the orbit. Medially it is in contact with the frontal, posteriorly with a lateral flange of the parietal; laterally it is barely in contact with the postorbital.

The postorbital is centered at the point of meeting of the postorbital bar with the bar of bone separating upper and lower temporal openings. The bone is here thickened, with a prominent external knob, posterior and dorsal to which it is gently concave externally. A ventral flange forms much of the posterior margin of the orbit, overlapping the jugal anteriorly. Above, the bone is in contact with postfrontal and parietal along the upper part of the postorbital bar. A posterior flange joins with the squamosal in the formation of the bar separating the temporal openings.

The jugal is of typical construction, its main ramus lying below the orbit and extending from a point anterior to the orbit backward to a contact with the quadratojugal below the lateral

temporal fenestra. Behind the orbit a ramus ascends, slimming as it goes, behind the lower branch of the postorbital.

The squamosal is a complex element. Its structural center lies at the posterior end of the bar separating the two temporal fenestrae. Anterodorsally a thin but deep flange extends forward to overlap laterally the posterolateral extension of the parietal. Anterolaterally a ramus extends forward to form, with the postorbital, the bar between the temporal openings. A backward extension of the bone from its center affords a broad area of articulation for the paroccipital process. Beneath this region the concave ventral surface of the bone supports the head of the quadrate. Forward and somewhat ventrally from this region a broad flange of bone forms a firm union with the dorsal end of the quadratojugal. In many pseudosuchians this flange forms the upper half of a V-shaped posterior border of the lateral temporal fenestra. Here, however, (as previously noted) an unusual condition exists. This flange turns so sharply forward that the upper half of the "normal" lateral opening is obliterated, and the flange is apposed to the postorbital, which forms the anterior margin of the upper part of the lateral opening under "normal" conditions.

The quadratojugal is a well-developed element. It forms the posterior part of the skull rim below the lateral temporal fenestra, between jugal and quadrate. A broad ramus extends upward and forward posterior to the lateral fenestra to terminate beneath the anteroventral ramus of the squamosal. The quadrate is highly developed. It presents a convex, transversely broadened, articular surface for the lower jaw on the under side of its posterior termination. From the medial edge of the articular area a sharply defined ridge runs upward and somewhat forward to terminate beneath the squamosal. The quadrate is broadly developed lateral to this ridge for nearly the entire height of the bone; this area is somewhat concave in transverse section. The lateral margin of the quadrate is in contact with the quadratojugal for most of the extent of the two bones. Not far above their ventral margins, however, there appears to be a small foramen, as in many early tetrapods, between the two bones, and quadrate and quadratojugal separate dorsally to reach their differing termini. Medial to the major vertical ridge on the quadrate there is seen a thin sheet of bone running medially for some distance in the position appropriate for the quadrate ramus of the pterygoid; at the bottom of this sheet is a curved ridge, running upward and anteromedially from the articular region of the

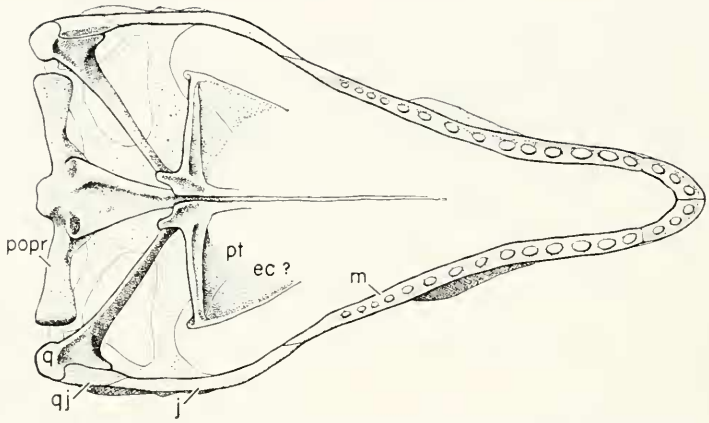

Figure 3. Palatal surface of the skull; the anterior portion of the palate is not preserved in available material. × 1.

quadrate. I am unable to determine how much of this bone pertains to the quadrate and how much to the pterygoid.

The upper rim of the occipital surface is formed by the two posterior flanges of the parietals, which curve backward, outward and somewhat downward to their lateral points of termination near the posterior angles of the squamosals. Between the two flanges, as noted earlier, is the small projecting postparietal; beneath, on either side, are the posttemporal fenestrae. Below and beneath the central part of these flanges is a broad plate of bone, the supraoccipital. It is essentially flat, but with a slight dorsoventral swelling in the mid-line. Fused with the supraoccipital on either side are the paroccipital processes, which extend outward to form a broad (but not tightly sutured) union with the squamosals. The paroccipital processes are relatively narrow proximally, expanding somewhat in vertical breadth distally and, except at their bases, thin anteroposteriorly; they are roughly oar-shaped. Exoccipitals and basioccipitals have been lost on MCZ 4118. They appear to be present in the crushed remains of the occiput in the holotype, but little detail can be made out.

The palatal surface is poorly preserved in available specimens. Posteriorly is a pair of well-developed basisphenoidal tubera. I have obtained no data regarding the lateral walls of the braincase in the otic region. No stapes has been discovered. The two quadrate rami of the conjoined quadrates and pterygoids slant strongly inward anteriorly, so that the two pterygoids are

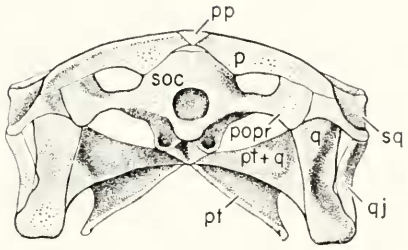

Figure 4. Occipital view of the skull. × 1.

apposed in the midline below the basisphenoid; it seems reasonably certain that movement of pterygoids on the braincase had been lost. A short backward median projection is present on each pterygoid at its point of apposition. Transverse pterygoid flanges are highly developed, extending straight out laterally and somewhat ventrally to occupy the total space available between the lower jaws when in occlusion. A pair of ridges extends outward along the under surface of each flange. Anterior to the flange, a curved sheet of bone, on which there appears to be a suture between pterygoid and ectopterygoid, slants upward anteriorly for a short distance. No data are available regarding the anterior portion of the palate.

The jaws (Figs. 2, 5) are slender. The symphysis is moderately elongate but shallow and is formed entirely by the dentaries. The dentary occupies practically the entire outer surface of the jaw for more than half its length. Posteriorly the dentary has a V-shaped suture with the surangular dorsally and a diagonal suture with the angular ventrally. Between dentary and surangular above and angular below is a typical archosaur lateral mandibular fenestra. There is a well-developed retroarticular process behind the broadly concave articular cavity. A splenial is well developed, occupying a considerable area on the inner surface of the jaw, but is barely visible externally. The prearticular forms a buttress at the anterior margin of the articular surface and thence extends forward and downward below the adductor fossa. The jaw is strongly compressed mediolaterally, and hence the large fossa looks medially rather than dorsally. The dorsal rim of the fossa is marked by a well-developed longitudinal ridge along the upper margin of the surangular. I am not sure whether or not a coronoid was present at the anterior margin of the fossa; the material is imperfect but suggests that a thin sheet of coronoid may have been present anterior to the adductor fossa.

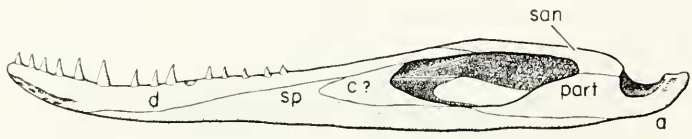

Figure 5. Internal surface of the lower jaw. Sutures in the presumed coronoid region are uncertain. × 1.

The teeth of *Gracilisuchus* are of the typical thecodont type common among carnivorous archosaurs — somewhat flattened mediolaterally, sharp-pointed and curved somewhat posteriorly toward their tips. Only two small teeth are definitely preserved in the only specimen in which the premaxillae are present, but the space available suggests the presence of a third. A disarticulated maxilla of the type skull has fortunately preserved a nearly complete series of maxillary teeth, not fully thecodont. About 14 appear to have been present. From a small first tooth, there is a steady increase in size to the fourth, following which there is a steady reduction to small elements for the last half dozen of the series. The lower teeth are not fully preserved, but the evidence suggests that none were of large size, and that there was a rather even row of small teeth, spaced about 2.5 mm apart, to a total of 16 or so.

AXIAL SKELETON

A considerable amount of vertebral material of *Gracilisuchus* is present in the collection. The holotype when entombed possessed a complete articulated presacral series (Fig. 6). However, the nodule in which the specimen was preserved had undergone considerable damage before collection. A split had occurred in the nodule that slanted back down most of the length of the series of dorsal vertebrae and, with the loss of a large chip adjacent to it, caused the complete loss of the posterior cervical and anterior dorsal vertebrae and damage to the remainder of the dorsals. The second and third vertebrae from the end of the series are obviously sacrals. Most of the ribs of the right side are preserved in their original position. This aids greatly in determining the spacing of the missing vertebrae, as does, further, a calculation, from known lengths of cervical and posterior dorsals, of the number of vertebrae contained in the missing segment of the column. As a result, it seems rather certain that 23 presacrals were present in life — a reasonable thecodont count.

Figure 6. The holotype skeleton, in dorsal view. × 1/2.

In MCZ 4118 a number of short sequences of articulated vertebrae are present:

(1) A series of cervicals articulated with the fragmentary skull.

(2) Six articulated centra that appear to lie in the cervical-dorsal transition.

(3) Six vertebrae, three well preserved, lying close to the skull-cervical series; they are probably anterior dorsals.

(4) Five poorly preserved vertebrae, presumably dorsals.

(5) Nine vertebrae, probably posterior dorsals, sacrals and proximal caudals.

(6) Two poorly preserved dorsals, with ribs.

(7) Ten caudals, probably from the middle of the tail.

These series will be referred to below by number. Excluding no. 6, 35 vertebrae are present, most of which are surely presacrals. It is obvious that not all belong to one individual; some, apart from nos. 1 and 3, may have been associated with MCZ 4117, a skull found in the same nodule.

The Tucumán specimen mentioned above has present much of the column; in all observed respects it agrees well with the material from the holotype and no. 4118. MCZ 4116 contains a mélange of vertebral material, some of which appears to belong to *Gracilisuchus* (as does the skull included in this slab).

The cervicals are best seen in the series (no. 1) connected with the skull remains in 4118 (Fig. 7); a similar but less well-preserved series is present in the holotype. The atlas is partially concealed by other materials, but as far as can be seen, has a typical archosaur structure — a well-developed intercentrum, above which are paired neural arches, and back of this articular ring a small atlas centrum and a small axis intercentrum. The axis has a well-developed centrum and a neural arch and spine of stout construction. The vertebrae in the cervical region posterior to the axis are similar in pattern, but with a less expanded neural spine. In these vertebrae the spines slant forward dorsally; in typical members of this series they are, as preserved, covered by dermal armor at their tips; isolated posterior cervicals and anterior dorsals show that their tips were flattened, obviously for close apposition of armor scutes. Two well-developed apophyses for rib articulation are seen on each centrum from the axis backward. The capitular articulation is a short parapophysis developed low down anteriorly on the centrum and terminating in a round articular area. The area for tubercular attachment is a short transverse process slanting sharply down-

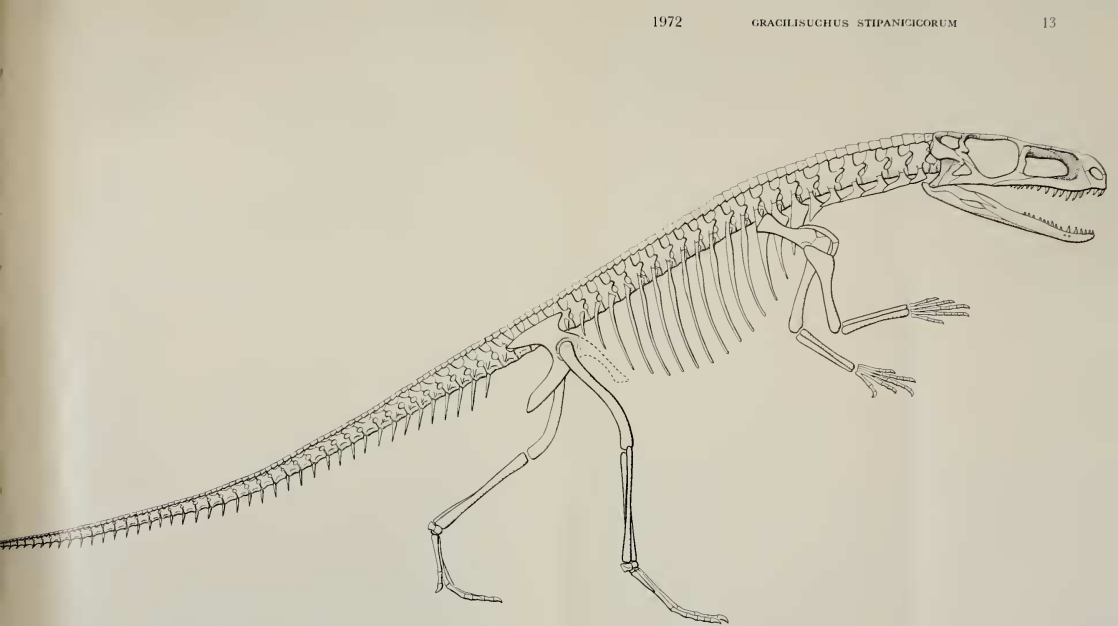

Plate 1. Skeleton of *Gracilisuchus stipanicicorum*, restored. Dermal shoulder elements, manus, pubis, and distal part of tail unknown. × 1/2.

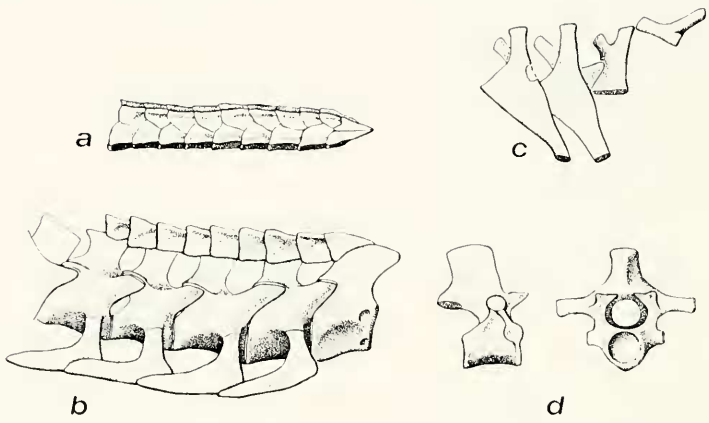

Figure 7. *a*, Dorsal scutes of the cervical region, seen from above. *b*, The cervical region in side view (the atlas is not included). *c*, Incomplete ribs of the right side, transitional between cervical and dorsal series. *d*, A dorsal vertebra in lateral and anterior views. All from MCZ 4118. × 1.

ward from a point near the anterior edge of the neural arch. By the time the seventh vertebra is reached, the diapophysis has moved to a point somewhat higher on the arch and is directed more laterally. The parapophysis, however, appears to have been persistently ventral in position in the cervical region. No intercentra are preserved back of the atlas. In MCZ 4118 cervicals two to six are completely preserved, the seventh is incomplete; in the holotype six vertebrae are similarly preserved. In MCZ 4118 the typical cervicals average 10.5 mm in length and in the holotype the length is approximately the same. From the axis back all centra are keeled ventrally.

Of the posterior cervicals and anterior dorsals, nothing can be made out on the holotype. Associated, however, with 4118 are two series of vertebrae that appear to represent this area. One such series (no. 2) includes six articulated centra and a fraction of the next posterior centrum; central lengths here average 8.5 mm. Neural arches and spines are not preserved, but ribs are present on four, the first two well preserved. Since the first rib of the series resembles that which (as noted later) appears to be associated with vertebra 7 in the holotype, it is reasonable to assume that this series includes vertebrae 7–12 as well as part of centrum 13. In presumed vertebrae 7–9 the capitulum still articulates well down the side of the centrum, and the build of

tubercular process indicates that in these segments the transverse process still slanted strongly downward.

Further vertebrae from the anterior part of the column are present in series no. 3, three in articulation and well preserved. We are dealing here with typical dorsals (Fig. 7). Vertebral lengths average close to 8 mm. Rib attachments are markedly different from those of the series described above. The diapophyses now extend directly out from the arches. In the first of the three complete vertebrae the parapophysis lies about at the boundary between centrum and arch at the anterior edge of the vertebra; in the third member of the series, the parapophysis is well up on the side of the arch, not far below and anterior to the base of the diapophysis. The neural spines are broad anteroposteriorly, but low, with a height of but 7 mm above the zygapophysis. Their upper ends are broadly oval, for apposition to the dorsal armor. In the arch region the surface is poorly preserved, so that little can be seen regarding rib articulations.

Series 4, 5 and 6 are poorly preserved and crushed, so that it is difficult to determine the nature of the apophyses, and no ribs are attached, except in no. 6 (where the vertebrae show little). An ilium lies close to the posterior end of series 5, suggesting that this sequence may include proximal caudals and sacrals as well as posterior dorsals. No chevrons are present, and the condition of preservation of the lateral surfaces of the vertebrae is such that it is impossible to determine whether sacrals are included. It seems clear that, as in archosaurs generally, the capitular articulation has joined the tubercular one in originating from the transverse process; details, however, are not clear. In no. 5 central lengths are about 8 mm. In series 6 the mean central length is a little over 7 mm; the neural spines are broad anteroposteriorly but low, rising only about 5 mm above the zygapophyses, and the total height of a vertebra is about 13 mm. As preserved, the centra in series 5 and 6 are prominently keeled ventrally and thin from side to side, but this may be due to post-mortem compression.

One further series of vertebrae on the 4118 slab, no. 7, includes 10 articulated caudal vertebrae, evidently from the midportion of the tail. Central length of an anterior member of this series is 6 mm, that of posterior members 5.5 mm. Chevrons are present, the most anterior one being 10.5 mm in length; in contrast, that between the sixth and seventh of the series is but 7 mm long. The vertebrae are still fairly tall, an anterior member measuring 8 mm from bottom of centrum to zygapophysis,

while at the posterior end of the series this height is somewhat reduced. The first two members of the series have well-developed spines, slanting backward and rising to a vertical height above the zygapophyses of 6 mm. Posteriorly the spines are reduced, and at the end of the series are merely low triangles above the zygapophyses.

As noted earlier, sacral vertebrae are present, although poorly preserved, in the type. The Tucumán specimen (Fig. 8) includes well-preserved sacrals in articulation with ilia. Beyond them are 16 articulated caudal vertebrae. Anterior members of this series have a central length of about 9 mm, posterior segments about 7.5 mm. In the anterior members of the series the neural spines are narrow anteroposteriorly, but moderately high, with heights of 10 mm or so above the zygapophyses; they are tilted posteriorly. In the posterior members of this series the spines are much reduced in height. The first chevron is present between vertebrae 3 and 4. Most chevrons are imperfect distally, but that between vertebrae 8 and 9 is 17 mm long. If we compare this series with that of no. 7 in MCZ 4118 — and take into account the larger size of the Tucumán specimen — it would seem that the 4118 series includes segments comparable to the posterior part of the Tucumán series.

Vertebrae present on the holotype slab, although disconnected from the main specimen, appear to represent much of the length of the tail. One series of seven vertebrae, and part of an eighth, is articulated and for the most part well preserved. Each measures 8 mm in length. The neural spines are low, and capped by dermal plates to give a total height of about 8 mm above the level of the zygapophyses. The transverse processes are incompletely preserved. There then follows a series of about 14 partially disarticulated and poorly preserved vertebrae which, as indicated by long transverse processes, are definitely caudals. Of several that are moderately well preserved, the length of the centrum is, again, about 8 mm; the width over the transverse processes is 15 mm. Beginning near the end of this series is a further series of about 15 poorly preserved caudals of smaller size, with lengths of 5.5 to 6 mm in the distal members. There is thus definite evidence of 39 caudals making up a considerable part of the presumed length of the tail.

Cervical ribs (Fig. 7) are well seen in both 4118 and the holotype. There is no evidence as to the presence or absence of an atlantal rib. Typical members have the highly specialized pattern developed among certain early archosaurs and retained

today in crocodilians. Each rib is essentially plow-shaped, the two "handles" represented by converging rami running outward from parapophysis and diapophysis. The "blade" of the plow, formed distally by the union of the two "handles," includes a short point anteriorly and a long posterior extension. In typical cervicals each "blade" overlaps its more posterior neighbor to make a continuous rib series from the axis as far back, at least, as vertebra 7. As in the case of the vertebrae, the rib transition to the dorsal series is somewhat uncertain. In series 2 of no. 4118 (Fig. 7), four incomplete ribs are present on the left, and one on the right. The first three ribs extend strongly forward from the point of union of capitulum and tuberculum to form a triangular sheet of bone, the front end of which underlies the next anterior rib. The main shaft of the rib extends outward and downward in line with the tuberculum, rather than turning backward as in typical cervicals; shaft lengths are uncertain. The width of the proximal rib expansion (presumably associated with serratus muscles) decreases from the first to the third of the series, and rib 4 appears to lack any expansion.

In the holotype most of the dorsal ribs are preserved. Mid-dorsals have average lengths of 62 mm. There is, as expected, a diminution in length toward the sacrum. The fourth presacral rib measures but about 46 mm, the three following, as preserved, 39, 18 and 10 mm. The main shaft of typical dorsal ribs averages but about 1 mm in diameter for most of their length; they thicken somewhat toward their heads. The direct proximal course of each rib is toward the tubercular attachment; the capitular head slants downward medially from the course of the shaft to extend several millimeters further than the tuberculum. The ribs show considerable curvature proximally, little distally, thus suggesting (reasonably) that the trunk was relatively high and narrow in its proportions.

DERMAL ARMOR

As in many other pseudosuchians, *Gracilisuchus* was armored dorsally. Best preserved is the armor of the cervical region (Fig. 7). The plates, thin but highly sculptured, are paired, and approximately two pairs are present for each vertebral segment. When articulated, the series of plates form a dorsal shield with a flat area, about 5 mm wide, running longitudinally down the column over the neural spines and with, on either side, a vertical sheathing about 5 mm in height. A sharp ridge separates

dorsal and lateral portions of each plate laterally; each plate overlaps its posterior neighbor. The plates of either side join to form the dorsal area, each member of a pair overlapping dorsally (as laterally) its posterior neighbor, and with members of each pair overlapping its partner; in 4118 the left plates overlap the right. Anteriorly, over the atlas region, the plates appear to narrow dorsally as a pointed terminus, but details are uncertain.

The plating of the dorsal region is imperfectly preserved in available material. Only small plate fragments are present in the isolated dorsal series found with 4118. In the badly preserved dorsal series of the holotype, a lateral plate covering is seen in the area of the third to fifth presacral neural spines, indicating that the type of plating seen in the cervical region was continued down the back. In the holotype the series of proximal caudals described definitely carry dorsal scutes, although details are somewhat obscure.

No articulated series of abdominal ribs is preserved, but in the holotype a scattered series of typical archosaur gastralia are present in the area near the shoulder girdle and front legs described above. Those gastralia that are completely preserved measure about 35 mm in length. They are essentially straight for most of their length, but gently curved toward their presumed medial ends.

APPENDICULAR SKELETON

Much of the girdles and appendages are preserved, although partially disarticulated, in the holotype; a number of elements are preserved in MCZ 4118; disarticulated elements are to be found on the MCZ 4116 slab.

In *Gracilisuchus* the front limbs are much shorter than the hind, and hence, as expected, the shoulder girdle is of small size. A right scapulocoracoid (Fig. 8) is present in the type (as well as an incomplete left scapula). The height of the scapula is 24 mm. The structure is typically thecodont; the scapular blade is slender, but ventrally the anteroposterior width increases to 11 mm before the anterior margin retreats to the clearly marked scapulocoracoid suture. The back margin ventrally is strongly bevelled off for a prominent area of articulation for the humerus, facing diagonally outward and backward. A somewhat less marked articular area is present below on the coracoid. This latter element, with rounded borders, is much broader anteroposteriorly than dorsoventrally, the measurements concerned

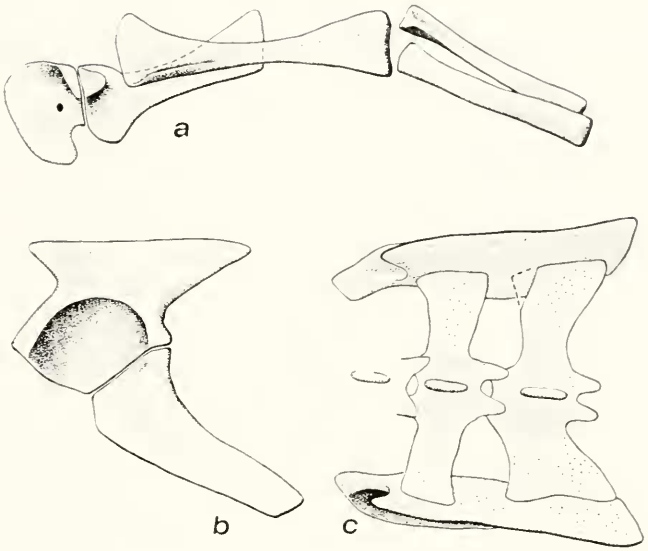

Figure 8. *a*, Right shoulder girdle, humerus, radius, and ulna. From the holotype. *b*, Left ilium and ischium. *c*, Sacral ribs and ilia, seen from above. From a specimen in the Instituto Lillo, Tucumán. All × 1.

being 17 mm and 11 mm; there is thus no suggestion of crocodiloid build. Just below the suture with the scapula the coracoid is slightly notched anteriorly; below this point the bone expands anteriorly to a considerable degree. A coracoid foramen is present anteroventral to the articular area. A similar scapulocoracoid is present on MCZ 4116. Of dermal girdle elements, none are identifiable with certainty in the material studied. Of pelvic girdle elements (Fig. 8), ilia are present in the holotype, in MCZ 4116, MCZ 4118, and in the Tucumán specimen mentioned. The element is of generalized thecodont proportions, with an iliac blade extending only a short distance anterior to the acetabulum, but much better developed posteriorly. The upper edge of the blade is thin; below, however, it swells convexly on the inner surface to allow for excavation of the acetabulum externally. The acetabular margin, semicircular in outline, is well defined; it is deeply incised into the bone, particularly anteriorly, where the margin develops as an overhanging shelf. The lower margin of the bone is convex in outline, with some differentiation of pubic and ischiadic contacts. It is obvious that the pelvis was imperforate.

Little evidence of the ventral elements of the girdle can be identified in the material. I have found nothing in the available specimens that I can identify with confidence as pertaining to the pubis. Imperfectly seen ischia are present in the Tucumán specimen and a pair of conjoined ischia are present in MCZ 4116. Unfortunately, the front margins of the ischia are imperfectly preserved, so that only a fraction of the acetabular margin is present and nothing can be said concerning the relations of ischium and pubis. The bones are bladelike, tapering posteriorly and having a long median contact between the two elements.

Of the short front legs, the long bones of both sides are present in semi-articulated fashion close to the right scapulocoracoid of the holotype (Fig. 8). A humerus is present in 4118, and two incompletely preserved specimens are present in 4116. Except for the last, the bones are exposed from the ventral surface. The structure is that typical of primitive archosaurs generally — hourglass shaped, moderately expanded at either end, and constricted at mid-length of the shaft. There is a well-developed deltopectoral crest. Distally, there is a circular convex area for articulation with the head of the radius; lateral to this the bone is somewhat notched for reception of the olecranon.

The right radius and ulna (Fig. 8) are present and articulated with the humerus in the holotype; the left radius and ulna are incomplete distally. I have not been able to identify these elements in other specimens. As preserved, they show little character; both are slender elongate cylinders. The ulna is somewhat expanded proximally, but there is no olecranon ossification.

Regrettably there are no identifiable remains of the manus preserved.

Femora (Fig. 9a) are present in the holotype, nos. 4116, 4118, and the Tucumán specimen mentioned earlier; in the 4116 slab there are four femora of appropriate size and shape, indicating the presence of two individuals of *Gracilisuchus*. The bone has the typical sigmoid curvature of a proper archosaur. The head is turned somewhat medially from the shaft, but this curvature is less pronounced and the distinction between head and shaft less marked than in *Lagosuchus*, for example. There is no evidence of the presence of a "fourth trochanter." Tibia and fibula are present in articulation with the femur on the right side of the holotype, and these elements are present also in nos. 4116, 4118, and the Tucumán specimen (Fig. 9b and c). These elements are long and slender but where associated are nevertheless somewhat shorter than the femur. As always, the tibia is

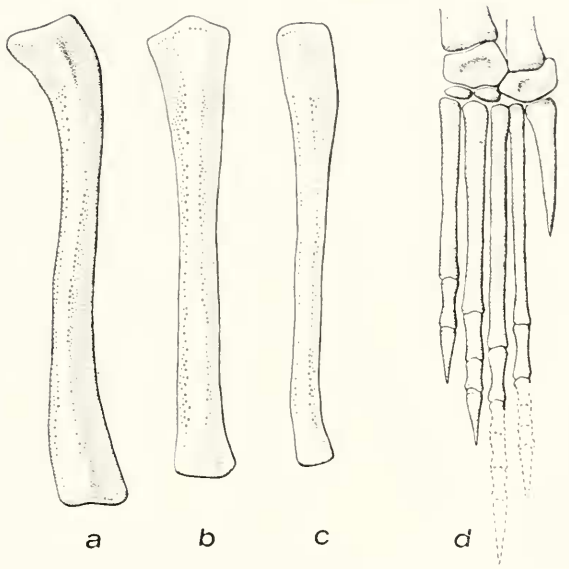

Figure 9. *a, b, c,* Left femur, tibia, and fibula. *d,* Left pes, composite. All × 1.

much stronger than the fibula, with an expanded triangular head, a well-developed cnemial crest, and a broadly oval distal area for astragalar articulation. The fibula is moderately broad but flattened throughout, with a gently sigmoid curvature.

The pes (Fig. 9d) is incompletely known. In the foot pertaining to the right leg of the holotype the usual two small distal tarsals are present. But little is preserved of the two proximal tarsals, and nothing worthy of description can be made out from tarsal remains associated with tibia and fibula in MCZ 4118. Astragalus and calcaneum are, however, moderately well preserved in the Tucumán skeleton mentioned earlier. The astragalus is a stout element, broad mediolaterally and moderately deep proximodistally; the anterior surface is somewhat concave. At its lateral margin the astragalus, as articulated, is in contact with the fibula, and below this area a diagonal surface of contact with the calcaneum is present. The calcaneum is less developed proximodistally. Details of the astragalocalcanear articulation cannot be determined; the calcaneum, however, had a well-developed "heel" in the fashion of crocodilians and many pseudosuchians.

Data on the digits of the pes are available only in the holotype and the Tucumán skeleton; the foot of the former is of the right side, of the latter, the left. Neither is complete distally. In the holotype metatarsals I–IV are present, but metatarsal IV is incomplete. Metatarsal IV is notably more slender than I–III. Metatarsal lengths as preserved are: 12 +, 23, 28 and 24 + mm. In the Tucumán specimen all five metatarsals are present, with lengths of 24, 28, 33, 32 and 18 mm; metatarsal V is of the "hooked" type, pointed distally. On the holotype no phalanges are present on toe I, but on digit II all three phalanges are present, with lengths of 7, 6, and 8 mm. On toe III a single phalanx is imperfectly preserved; no digits are present with metatarsal IV. In the Tucumán specimen, the two phalanges of digit I are present with lengths of 6 and 8 mm. On digit II all three phalanges are present, the third incomplete, the first two with lengths of 7 and 4 mm. On digit III three phalanges are present, but only the first, with a length of 10 mm, is well preserved. With digit IV there is found only a single phalanx, 7 mm long.

Allowing for a disparity in size of about 20 percent, the data from the two specimens agree well and allow a complete construction of the foot except for the more distal phalanges of toes III and IV. Assuming that as regards these phalanges, the pattern is that found in other advanced thecodonts and primitive saurischians, the restoration shown in Figure 9d cannot be far from the actual condition. It may be noted that in the specimens with articulated foot material, the toes are closely appressed to one another, as in my figure, with no trace of the fan-shaped spreading seen in many reptiles.

RESTORATION

Between the various available specimens, nearly the entire skeletal structure of *Gracilisuchus* is identifiable, and hence a skeletal restoration is justified (Plate 1). As usual in archosaurs in which the front limbs are notably shorter than the hind, the question arises as to whether a bipedal or quadrupedal pose is suitable. In the case of *Chanaresuchus* (Romer, 1972) I restored the animal as a quadruped, despite considerable disparity in limb lengths, because of the probably amphibious, crocodile-like nature of the animal. *Gracilisuchus*, as already mentioned (and discussed below), is quite surely a relative of *Ornithosuchus*, and I have followed Walker's restoration of that reptile in restoring *Gracilisuchus* as a biped. It is possible that the normal

pose of *Gracilisuchus* was a quadrupedal one; however, I feel sure that, if pressed, this animal was able to run in the bipedal manner in which I have restored it.

RELATIONSHIPS

It is quite clear, I think, that *Gracilisuchus* is a relative of *Ornithosuchus* of the later Elgin beds of Scotland, ably described by Walker in 1964. The skull structure is closely comparable in most regards, as are various postcranial features. Walker has suggested certain late Triassic saurischian genera as possible *Ornithosuchus* relatives which might belong with this genus in a common family Ornithosuchidae, and Bonaparte (1969b) has recognized two Argentinian genera (*Venaticosuchus* and *Riojasuchus*) that seem quite surely to belong in this family. *Gracilisuchus*, from the Chañares beds — quite probably Anisian in age — is the oldest (and smallest) of forms that may pertain to this apparently common and perhaps widespread Triassic family. In a few features (such as the partial closure of the lateral temporal fenestra) the genus *Gracilisuchus* is perhaps slightly aberrant, but it seems quite surely close to the base of this stock.

Walker argues further that *Ornithosuchus* is a carnosaur — a proper dinosaur rather than a thecodont ancestor of dinosaurs. I provisionally adopted this interpretation when I published my 1966 edition of *Vertebrate Paleontology*. I confess, however, to now having reservations on this assignment (cf. Bonaparte, 1969a). Certainly the ornithosuchids show a number of features that might be expected in a carnosaur ancestor. But in certain features *Gracilisuchus* surely is below a proper dinosaur "grade" in structure: the apparent complete closure of the acetabulum, for example. Again, saurischians are completely devoid of armor, and I would be loath to believe that the dorsal armor seen in *Gracilisuchus* and *Ornithosuchus* would have been developed and secondarily lost. I do not wish to enter the controversy over the evolution of tarsal structure, but the presence in ornithosuchians of a "crocodilian" type of tarsus is, to say the least, an argument against placing the family in the Carnosauria, although not necessarily debarring the group from an ancestral position. Certainly the ornithosuchids show a trend in development that is in many ways similar to that which led to the carnosaurs. But for the time, it is, I think, better to regard them as forms related to and paralleling the line leading to the carnosaurs rather than members of that group.

As our knowledge of thecodonts increases (as it is currently doing at a rapid rate), it seems clear that while crocodilians, pterosaurs, bird ancestors and ornithischians have struck off on a variety of "tangents," the saurischians show merely an improvement on structural patterns already evident among the thecodonts. It has been generally held that the Saurischia are a "natural" order, monophyletic in origin. But recently it has been advocated (Charig *et al.*, 1965) that the sauropods are only distantly related to the "theropods" and may have arisen independently from ancestral thecodonts, and it is not impossible that among "theropods," carnosaurs and coelurosaurs may have had independent origins (cf. Bonaparte, 1969a). I am constitutionally allergic to unnecessary advocacy of polyphyletism, but I fear that we are as yet far from a solution to questions of relationships between various thecodont and saurischian groups.

TABLE I

Length of limb bones, in mm

	Holotype	MCZ 4118	MCZ 4116	Tucumán specimen
Humerus	38	44	44	—
Radius	30	—	—	—
Ulna	31	—	—	—
Femur	58, 60	68	64, 62, 61, 60	81
Tibia	56	59, 64	61, 56	73
Fibula	55	64	47+	65

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